Vol. 73, pp. 183–194 30 December 1960

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

THE DISCOVERY OF A FRESHWATER OPISTHOBRANCHIATE MOLLUSK, *ACOCHLIDIUM AMBOINENSE* STRUBELL, IN THE PALAU ISLANDS

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Two peculiar shell-less opisthobranchs obtained by A. Strubell in a stream in Amboina were briefly described by the collector and named *Acochlidium amboinense* and *A. paradoxum* (Strubell, 1892: 62). Prof. Max Weber collected some animals similar to the first of these in the mouth of a river in Flores, which were described by Bergh as *Hedyle weberi* (Bergh, 1895: 4). Strubell's deficient description of *Acochlidium amboinense* was supplemented by Bücking's study of the original specimens, making it clear that *A. amboinense* and *H. weberi* are distinct species of one genus (Bücking, 1933: 549–582).

The latter, properly called *Acochlidium weberi* (Bergh), has recently been reported from Sumba by van Benthem Jutting (1955: 55) but *A. amboinense* has not been seen again. Some animals very similar to it in general appearance were discovered by one of us (Fehlmann) during the course of a detailed ecological survey of a stream on the southwest coast of Babelthuap, the largest of the Palau Islands, in September of 1957. When these proved to be of unusual interest, additional specimens were collected during a subsequent visit in October, 1958, and color photographs were made of the living animals. We were then able to confirm the identification as *Acochlidium amboinense* Strubell.

It is not our purpose to give a history of these remarkable freshwater opisthobranchs, which already has been done by

Bücking (1933) and Odhner (1937, 1938), but to report the occurrence of the genus in a stream in the Palau Islands, nearly a thousand miles from the original locality in Amboina, and separated by 500 miles of the Pacific Ocean from other large islands where it reasonably might be expected.

We are indebted to Harold W. Harry, who undertook the preliminary dissections of the first lot of specimens obtained and who made tentative determination of their taxonomic position. We are grateful also to W. S. S. van Benthem Jutting van der Feen of the Zoological Society of Amsterdam, who called our attention to her paper on freshwater mollusks from Sumba and showed one of us (Bayer) the specimens of *Acochlidium weberi* reported therein, and to Harald A. Rehder of the Smithsonian Institution, who gave freely of his time to help us in the search for literature and to read the manuscript. The field work that provided our specimens was aided by contract NR 160 321 between the Office of Naval Research, Department of the Navy, and the National Academy of Sciences—National Research Council, under the auspices of the Pacific Science Board, and by contract AT (04-3)-102 between the United States Atomic Energy Commission and Stanford University. Logistic aid and permission to conduct field work in the Palau Islands were provided by the Trust Territory of The Pacific Islands, United States Department of the Interior. We are, as always, grateful for the encouragement and support of the George Vanderbilt Foundation of Stanford University, and of the Smithsonian Institution, Washington, D. C.

Genus *Acochlidium* Strubell

Acochlidium Strubell 1892, Verhandl. naturh. Ver. preuss. Rheinlande, 49. Jg., Sitzung der niederrheinischen Ges. 13. Juni 1892: 62.
Hedyle Bergh 1895, Verhandl. zool. bot. Ges. Wien 45: 4.
not *Hedyle* Guénée 1857; not *Hedyle* Malmgren 1865.
Acochlidium, Odhner 1937, Zool. Anz. 120: 52, 64.
Acochlidium, Odhner 1938, Basteria 3: 5–11 (passim).

Hedyle, the generic name applied to these naked snails by Bergh in 1895 is not only a junior subjective synonym of *Acochlidium* Strubell, but is also twice preoccupied. In view of the fact that Strubell did provide some morphological information about his animals, and since a name is not nude unless it is devoid of all descriptive matter, the names he pro-

posed are not nomina nuda. We must therefore disagree with Odhner in attributing authorship to Bücking.

The external morphology of the specimens from the Palau Islands is very close to that of *Acochlidium amboinense* as redescribed by Bücking, and gross dissections demonstrate that anatomical characters, notably the radula, the penial armature, and the calcareous spicules, are also in close agreement. The discrepancies are so small as to be of little consequence, particularly in view of the fact that they may well be the result of different artistic representation of the features in question.

Acochlidium amboinense Strubell

(Figs. 1 and 2)

Acochlidium amboinense Strubell 1892, Verhandl. naturh. Ver. preuss. Rheinlande, 49. Jg., Sitzung der niederrheinischen Ges. 13. Juni 1892: 62.

Hedyle amboinensis, Bücking 1933, Zool. Jahrb. Syst. 64: 552, Figs. 1–27; pl. 2.

Acochlidium amboinense, Odhner 1937, Zool. Anz. 120: 52, 64.

Acochlidium amboinense, Odhner 1938, Basteria 3: 5–11, passim.

Material examined: Three lots of specimens, all from the same locality in the Palau Islands: south fork of Arakitaoch stream, Airai Municipality, Babelthuap Island; cascade zone 150–190 feet above sea level; collected by H. A. Fehlmann and Sumang Yachad, 12 September 1957 (5 specimens), 16 September 1957 (4 specimens), and 2 October 1958 (10 specimens).

Descriptive remarks: The living animals measure about 2.5 cm in length when extended and crawling (Fig. 1, a–c). They resemble the drawing of the living animal made by Strubell and published by Bücking (1933: pl. 2, Fig. 1; copied by Odhner, 1938: Fig. 5), with the exception of the attitude in which the tentacles are held, and the shape of the visceral sack ("Eingeweidesack"). Our drawings are ink stipple renderings traced from color photographs of actively crawling specimens, and therefore accurately represent the outline of the living animal including the shape of the visceral sack and the usual position of the tentacles.

Strubell's original sketch gives the impression that (1) the visceral sack is more or less auriculate anteriorly and thus shaped somewhat like a cordate leaf, and (2) the hepatic diverticula are visible as a rather distinct system of veins marking the surface of the visceral sack. Neither is the case in the specimens from Palau. The visceral sack has the shape shown in Figure 1, a–c, and has a perfectly smooth surface. There are no auriculate expansions at the anterior margin of the sack.

In life, the Palauan specimens were deep olive green, rather blotchy in the visceral sack, which is also flecked with white. The head and anterior part of the body in front of the attachment of the visceral sack are somewhat paler and streaked in the manner shown in Strubell's sketch. An oval, darker green area at the anterior end of the visceral

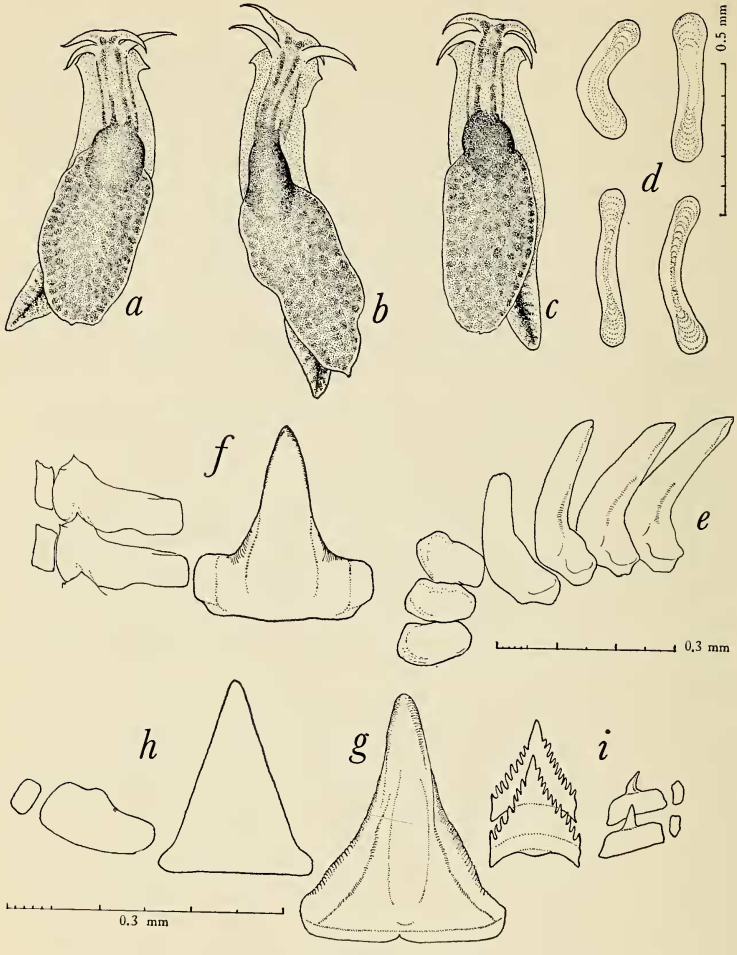

FIG. 1

sack indicates the position of the visceral mass. To judge by Strubell's figure, his specimens were a paler, brighter green than were the animals collected in Arakitaoch stream.

Measurements were not taken of the living specimens, due to pressure of time, and the preserved animals are so contracted and distorted that detailed measurements are not especially informative. However, the dimensions of some of the conspicuous features in topographic anatomy are given below in tabular form. The measurements of specimens collected in 1957 differ somewhat from the figures given for material taken

in 1958 owing to the fact that the latter were anesthetized by various means prior to fixation in formalin and have therefore retained more nearly normal shape.

Measurements (in mm) of *Acochlidium amboinense*

	TOTAL LENGTH	LENGTH OF VISCERAL SACK	WIDTH OF VISCERAL SACK	LENGTH OF FOOT	WIDTH OF FOOT
12 Sept. 1957	9	–	6	–	4
	9	–	6	–	4
	9	–	6	–	4
	9.5	–	7	–	4
	10	–	8	7	4.5
16 Sept. 1957	6	–	6	–	3.5
	8	–	5	–	4
	8	–	7.5	–	–
	10	–	5	6	4
2 Oct. 1958	11	–	8	–	4
	12	7	6	9	4
	12	9	6	10	4
	13	8	6	11	4
	14	10	9	10	4
	15	9	7.5	11	4.5
	16	12	7	7.5	4
	16	11	8	11	4.5
	–	9	8	12.5	–
	–	–	–	–	–

(Blanks indicate that the character was not measured because of distortion.)

Radula: According to Bücking's observations (1933: 558 et seq, Figs. 2a, 3, 4 and 5) the radula is bent around the lingual muscle and assumes the shape of the letter U lying on its side. It consists of five longitudinal rows: a middle row of teeth, on either side of which are two lateral rows of plates of chitinous material, which extend only along the ventral portion of the radula to the point where it bends back upon itself over the anterior end of the lingual muscle. In face view, the rachidian tooth is in the shape of an acute isosceles triangle 0.2 mm (200 micra) high and 0.15 mm (150 micra) wide. The thick, slightly curved cusp bends sharply backward from the base of the tooth, which is somewhat expanded laterally. There are no processes or thorns on the margin of the tooth. The inner lateral plates are all of irregular quadrangular form with rounded angles, measuring 0.04 × 0.11 mm; at the middle of the upper (i.e., posterior) margin they have a short "nasenartigen" process. The plates of the outer row are thin, small (0.02 × 0.025 mm) and are practically square.

Bücking records 52 rachidian teeth (24 on the ventral part of the

radula, 28 on the dorsal), 20 inner laterals in each row, and 10–15 outer laterals, a total of 112–122 teeth and plates in the complete radula.

Our observations upon the radulae of Palauan specimens agree in general with Bücking's description except as follows: the rachidian teeth measure about 0.27 mm in height instead of 0.2 mm; their sides are concave and finely serrated (Fig. 1 g), not straight and smooth, and when viewed in position on the radula the backward-bent cusp is much narrower than the base (Fig. 1 f). The wide, inner lateral plates bear a blunt process, with or without two or three denticles, toward the outer end, not the middle, of the upper margin; the lower edge of the following plate is recessed to accommodate this process. The small, squarish outer lateral plates often have a tiny denticle at the two upper corners (Fig. 1 f).

Contrary to Bücking's observations, inner lateral plates are present in all transverse rows, and the small outer lateral plates are present in all but the 10 youngest transverse rows where they have not yet been formed. In one of our preparations, the radula has 25 rachidian teeth with cusps completely worn off (those of the ventral part of the radula; see Fig. 1 e), 1 very much blunted by use, and 30 quite sharp and unworn (in the dorsal part of the radula), a total of 56; inner lateral plates are present in all 56 transverse rows, a total of 112; and outer laterals are completely formed in all but the 10 youngest rows (and even in these rows the outlines of the still incomplete plates can be seen), a total of 92 fully formed plates. The number of teeth and plates in the complete radula is therefore 260 (56 + 112 + 92).

It seems to us reasonably certain that these discrepancies are due to deficiencies in Bücking's observations rather than to any specific difference between our material and his. The outer rows of the radula are very delicate, especially toward the growing end, and the plates easily could have been overlooked if not completely torn off in the process of dissection. Moreover, Bücking's most detailed figures were drawn at such a low magnification that the marginal ornamentation of the rachidians was not noticed.

The radula of *Acochlidium weberi* as illustrated by Bergh shows a strong, triangular rachidian and two rows of lateral plates, as in *A. amboinense*. Aside from being smaller, the rachidian differs in having a conspicuously denticulated cusp, and the inner laterals bear a much stronger cusp situated in an approximately central position (Fig. 1 i). For the sake of comparison, Bergh's and Bücking's figures have been redrawn (Fig. 1, h and i) to the same scale as our own drawings (Fig. 1, f and g).

Spicules: A large number of spicules are situated in a ring around the esophagus and in the tissue of the foot, but not in the visceral sac. These bodies are transparent, cylindrical rods up to 0.5 mm in length, more or less bent and usually somewhat enlarged at the ends (Fig. 1 d). They are almost crystal clear, with only a slight milkiness, but a distinct core and evidence of concentric lamination can be seen in most of them. In

polarized light they show very slight birefringence. Spicules cannot be found in specimens preserved in formalin but they are conspicuous in alcoholic material, from which they can be dissected without difficulty. Although unaffected by alcohol, they dissolve readily and rapidly (in a matter of minutes) in ordinary tap water. They also suffer changes when mounted in balsam, but not uniformly. In a single preparation, some spicules may show signs of disintegration, whereas others remain unchanged. Further studies should be made to determine the nature and composition of these bodies.

Measurements of radular teeth and plates of *Acochlidium* (in mm)

	A. weberi°		*A. amboinense*†		*A. amboinense* (Palau)	
	Height	Max. width	Height	Max. width	Height	Max. width
Rachidian	0.11–0.12	0.09–0.1	0.2	0.15	0.24–0.27	0.22
Inner lateral	–	0.075	0.04	0.11	0.09	0.12
Outer lateral	–	0.02	0.025	0.02	0.055	0.03

° Measurements from Bergh.

† Measurements from Strubell, converted from micra.

Genital armature: According to Bücking's observations, the margin of the glans penis is furnished with a ring of about 15 hooks and thorns of a chitinous substance. His figure 7a shows 9 large thorns and 9 smaller hooks forming an incomplete ring around the glans. Our specimens, all of which are more or less contracted, show a semicircle of 14 large thorns in two rows around one side and 8 (in one specimen the base of a 9th, which seems to have been broken off, is clearly visible) smaller, slender hooks in a cluster on the opposite side. Terminal and lateral views of the most fully expanded preparation we were able to obtain are shown in Figure 2. Whether or not the double row of thorns and the cluster of hooks would spread out and form a single row during full expansion we are unable to say.

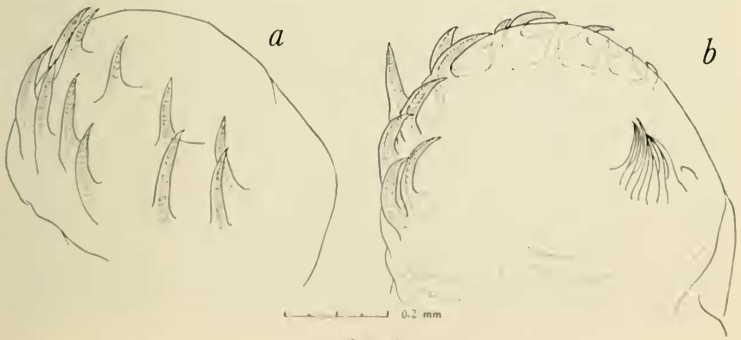

Fig. 2

Bücking does not describe the thorns and hooks in detail, saying only that the latter resemble shark's teeth in form and have the base drawn out into four hook-like processes. We have been unable to discern four basal processes, but the large thorns are joined to the integument by a pair of diverging roots. Bücking does not mention that each of the thorns is invested in a sheath of tissue from which a small part of the very sharp tip protrudes, as is the case in our material.

The structure of the hooks and thorns is similar to that described by Bergh (1895) for *Hedyle weberi,* although the thorns in that species, too, have three or four simple or branched roots. Both hooks and thorns are hollow, with a distinctly chambered core. In specimens of *H. weberi* 3 cm in length, the penis was from 3 to 8 mm long, with 15–20 hooks (corresponding to the thorns in Bücking's description) in a single row, and many smaller, more thorn-like hooks in two (here and there 3 or 4) rows. In Bücking's specimens of *Acochlidium amboinense,* as in ours, this organ was of somewhat more modest proportions.

Habitat and ecology: All specimens here reported were collected in the south fork of Arakitaoch stream in Airai Municipality on the lower west coast of Babelthuap, the largest island of the Palaus. The habitat is restricted to a very short "cascade zone" where the stream flows across exposed basaltic bedrock at an elevation of 150–190 feet above sea level (Fig. 3). The water was fresh (NaCl 17 parts per million) and had a temperature of 79°F at the time the specimens were collected.

Fig. 3

The specimens invariably were found on the few loose rocks that were lying in the shady stream bottom, covered by 1–12 inches of water; they were not found under the rocks or on the solid rock of the stream bed.

Of particular interest is the fact that *Acochlidium* were not found in the corresponding situation in the north fork of Arakitaoch stream, which, to all appearances, was ecologically identical. Neither were these snails found in the lower graded reaches of the stream or in the upper mangrove zone where the water becomes brackish, although these sections of the stream were collected and inspected with great care.

The fauna associated with *Acochlidium amboinense* in the cascade zone of Arakitaoch stream includes nine species of fishes (identified by H. A. Fehlmann), as follows (the most abundant are indicated by an asterisk):

Anguillidae: *Anguilla marmorata* Q. & G.
Gobiidae: *Stigmatogobius romeri* (M. Weber)°
Sicyopterus micrurus (Blkr.)
Stiphodon elegans (Steind.)°
Sicyopus zosterophorum (Blkr.)
Sicyopus n. sp.°
Eleotridae: *Eleotris fusca* (Bl. Schn.)°
Ophiocara aporos (Blkr.)
Bunaka gyrinoides (Blkr.)

Other animals associated with *Acochlidium* are the water striders *Microvelia notophora* Esaki, endemic in the Palau Islands, and a species of *Limnometra* (both determined by Jon L. Herring). Crickets of the genus *Tremellia* (family Gryllidae) also were abundant in the cascade zone, although they must have hidden themselves along the banks of the stream for they were rarely seen except after poisoning with rotenone when the crickets were dying and hopping around like pop corn. Aquatic lepidopteran larvae of the family Pyraustidae must also be common in the cascade zone, for they were found in large numbers in the stomachs of the common mountain goby (*Sicyopus* n. sp.), but they were not observed in the stream. A few nymphs of Ephemeroptera and Odonata were found under stones in the pools of the cascade zone.

Several species of shrimps (identified by L. B. Holthuis) were collected in the pools with *Acochlidium*, of which the most abundant were *Macrobrachium lar* (Fabricius) and *Atya pilipes* Newport. Present but scarce were *Macrobrachium placidulum* (de Man), *Atya spinipes* Newport, *Caridina typus* H. Milne Edwards, and *Caridina weberi* De Man, for which optimum conditions are probably located elsewhere in the stream. The grapsoid crab *Varuna litterata* (Fabricius) was also present (identified by Fenner A. Chace).

Other gastropods present were *Neritina pulligera* Lamarck and *N. cornea* Linnaeus, and unidentified species of *Stenomelania* and *Thiara*. The Neritinas were breeding freely and their egg cases bedecked their own shells and were found in patches all over the bedrock bottom of the stream. Egg cases and young snails were found only in this zone.

Zoogeographical remarks: The discovery of this distinctive freshwater opisthobranch on a high island well out in the Pacific Ocean, hundreds of miles from the type locality and considerably removed from other high islands where it conceivably could occur, is noteworthy in itself. When the biology of the animal has been thoroughly investigated, the zoogeographic implications of its distribution may assume considerable significance. A study of its life history, to determine whether or not there is a free-swimming marine larval stage to account for its distribution in fresh water on widely separated high islands obviously would be of the utmost importance. It will also be necessary to test the physiological tolerances of the adult animals to evaluate the possibility of chance dispersal through natural or artificial means, although the delicate body form and the ecologically restricted distribution do not speak for the exceptional lability and hardiness that such means of transport certainly would require.

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Explanation of Figures

Fig. 1. a–h, *Acochlidium amboinense* Strubell: a–c.—Animals extended and crawling; drawn from photographs. Actual length about 2.5 cm. d.—Spicules (enlarged according to adjacent 0.5 mm scale). e.—Rachidian teeth of portion of radula in region of active use; side view (enlarged according to 0.3 mm scale below). f.—Rachidian tooth and plates of one side of the radula; in situ (enlarged according to 0.3 mm scale below h). g.—Rachidian tooth dissected from radula; full face view (enlarged according to 0.3 mm scale below h). h.—Rachidian tooth and plates of one side of the radula (redrawn from Bücking to the same scale as Figs. f and g). i.—*Acochlidium weberi* (Bergh). Rachidian teeth and plates of one side of the radula (redrawn from Bergh to the same scale as Figs. f, g and h).

Fig. 2. *Acochlidium amboinense* Strubell. Retracted glans penis showing armature: a.—in lateral view. b.—in subterminal view.

Fig. 3. Arakitaoch Stream, Airai Municipality, Babelthuap, Palau Islands: cascade zone in south fork of stream, habitat of *Acochlidium amboinense* Strubell. Photo by H. A. Fehlmann, 12 Sept. 1957.